

SMALL SCALE DISTURBANCES AND SUCCESSIONAL DYNAMICS
IN A SHORTGRASS PLANT COMMUNITY:
INTERACTIONS OF DISTURBANCE CHARACTERISTICS

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ABSTRACT

The effects of interactions among disturbance characteristics on the successional dynamics of small scale disturbances in shortgrass plant communities of north central Colorado, USA, were evaluated by comparing naturally occurring and artificially produced disturbances of different type, seasonality, size, and location by soil texture.

The species composition on the two naturally occurring disturbances (western harvester ant mounds and small animal burrows) were similar one year after plant recovery began, and were different from the composition on the artificially produced plots. The high density and cover of perennials on ant mounds and animal burrows indicated that perennial organs were not killed by the clipping activity of harvester ants or by the pile of soil from burrowing animals. The majority of the cover on the artificially produced plots for two sites differing in soil texture, and most dates and sizes, was attributed to annuals. The importance of seasonality was indicated by the low cover of annuals and perennials on artificial plots produced in September.

Annuals and perennials responded differently to disturbance size. The density of annuals was not affected by the size of the disturbance while the significantly smaller cover values on the smallest compared to the largest plots indicated the effects of competition on the growth of annuals by plants surrounding the plots. Vegetative ingrowth from the edge of the plots resulted in significantly greater cover and density of perennial grasses and sedges on the smallest plots for most dates and both sites than plots of the two larger sizes. The cover and density of the most important perennial forb on the plots, *Sphaeralcea coccinea*, were highest in the center of the largest plots, or the farthest distance from potential competitive interactions with plants in the surrounding undisturbed community.

Although long term monitoring is necessary to evaluate the time required for each disturbed area to be dominated by a shortgrass plant community, the short term results suggest that animal burrows will have

the most rapid recovery time of the disturbance types studied and the largest artificially produced plots will have the slowest recovery time.

KEY WORDS: Disturbance, grassland, *Bouteloua gracilis*, animal burrows, ant mounds, succession.

INTRODUCTION

The disturbance regime of a plant community is composed of a number of disturbance types, each with its associated characteristics (Pickett & White 1985). The rate and pattern of reestablishment of plants following a disturbance is dependent on the life history characteristics of plants available to enter the disturbed site and the characteristics of the site (Sousa 1984). Most studies in grasslands have focused on the independent effects of different disturbance characteristics, including size (Davis & Cantlon 1969), seasonality (Perozzi & Bazzaz 1978) and type, such as ant mounds (King 1977), small burrowing animals (Platt 1975; Hobbs & Mooney 1985), drought (Albertson & Weaver 1944) and comparisons of several types (Collins & Barber 1985; Belsky 1987; Milchunas *et al.* unpublished).

Interactions among disturbance characteristics are also important (Collins & Uno 1983; Collins 1987). However, the nonuniformity of natural disturbances in characteristics such as size and seasonality causes difficulties in evaluating the separate effects of interacting disturbance characteristics. Several researchers have used manipulated plots to control for the heterogeneous characteristics commonly found associated with natural disturbances (Rapp & Rabinowitz 1985; Belsky 1986), but these simulated disturbances are likely not representative of all conditions found on natural disturbances. A comparison of natural disturbances with artificial disturbances of comparable, yet uniform characteristics, is necessary to evaluate the effects of different disturbance characteristics on successional dynamics.

In shortgrass steppe plant communities of the central and southern Great Plains of North America, most successional studies have focused on the independent effects of large scale disturbances, such as abandoned agricultural fields (Savage & Runyon 1937; Judd & Jackson 1939; Costello 1944; Judd 1974; Reichhardt 1982). Small patch producing disturbances are also important, but they have been largely ignored (Coffin & Lauenroth 1988). In shortgrass communities dominated by the perennial grass, blue grama [*Bouteloua gracilis* (H.B.K.) Lag. *ex* Griffiths], disturbances that kill at least one individual *B. gracilis* have the largest potential effect on community structure (Coffin & Lauenroth 1988).

Two examples of small scale disturbances of sufficient intensity and spatial scale to always kill at least one *Bouteloua gracilis* plant are western harvester ant mounds [*Pogonomyrmex occidentalis* (Cresson)] and burrows from small mammals, such as skunks (*Mephitis mephitis* and *Spilogale putorius*)

and badgers (*Taxidea taxus*). The effects of these two disturbance types on shortgrass communities are different. Western harvester ants remove the vegetation from around their mounds by clipping the plants below the soil surface while small mammals produce a mound of soil at the surface that covers and kills the vegetation.

Disturbance characteristics, such as size and seasonality, are correlated with different disturbance types and very likely affect succession. The texture of the soil on the disturbed site is also important to plant recovery in shortgrass communities because of the effects of soil texture on plant community composition (Anderson 1983).

Our objective was to evaluate the effects of interactions among disturbance characteristics on the successional dynamics of small scale disturbances in shortgrass steppe plant communities by comparing naturally occurring and artificially produced disturbances of different type, seasonality, size and location by soil texture.

METHODS

Data collection was conducted at the Central Plains Experimental Range (CPER) in north central Colorado, approximately 60 km northeast of Fort Collins (40° 49' N latitude, 107° 47' W longitude). Mean annual precipitation over the past 45 years was 311 mm (sd = 79 mm) and mean monthly temperatures ranged from -5° C in January to 22° C in July. Moderate grazing by cattle occurs throughout the area.

Two disturbance locations based on soil texture and with similar climate were chosen: a site with a coarse textured soil (sandy loam) and a site with a fine textured soil (clay to clay loam). Disturbance size was studied by producing artificial plots comparable in size and shape to the range of sizes observed for ant mounds and animal burrows (0.2-1.8 m²). Seasonality was evaluated by four recolonization dates: September 1 (1984), March 1, May 1 and July 1 (1985). Recolonization date refers either to the date when the artificial disturbances were produced or to the date when ant or animal activity ceased and plant recovery began on the mound or burrow.

Western harvester ant mounds

Previous studies in Wyoming (Kirkham & Fisser 1972) and observations at the CPER indicated that harvester ant mounds rarely occur on sites with fine textured soils; therefore, the location chosen to study plant recolonization on ant mounds was a site on a sandy loam soil. The surface area of each full size mound in a 1.5 ha area was estimated by measuring the longest diameter of each mound and the diameter perpendicular to the first diameter. Eight mounds were randomly assigned to each of the four recolonization dates (Coffin & Lauenroth unpublished).

During the time that western harvester ants inhabit a nest site, the ants inhibit plant growth on the mound by clipping the plants below the soil surface. Therefore, it was necessary to remove the ants in order to study the recolonization of plants on the mounds. Environmental conditions in the nest were altered by placing a plywood box over each of the eight mounds, two weeks prior to the September, May and July recolonization dates. This resulted in the ants relocating their nests. The plywood boxes were ineffective for the March recolonization date since harvester ants overwinter below the soil surface and do not become fully active until late March or mid April (Lavigne 1969). A biocide (Diazinon) was used to kill the ants of the eight mounds for the March date.

Small animal burrows

Observations at the CPER indicated that small animal burrows occur primarily on sites with coarse textured soils with a relatively low frequency of occurrence ($0.5 \text{ burrows ha}^{-1} \text{ y}^{-1}$ from Coffin & Lauenroth 1988). Therefore, a large area (5-10 ha) on a sandy loam soil was examined during the time of the study (September 1, 1984-July 1, 1985) for the occurrence of newly formed burrows. Seven burrows were found for one recolonization date, July (1985). Newly formed burrows were not found for the other three dates. Observations at the CPER also indicated that small burrowing animals do not inhibit plant growth on the mound of soil produced by the burrow; therefore plant recovery began immediately after the burrow was produced. The surface area of the mound of soil was estimated by measuring the longest diameter and the diameter perpendicular to the first diameter.

Artificial plots

Artificial plots were produced on two locations differing in soil texture: a coarse and a fine textured soil. Circular plots of three sizes (50, 100 and 150 cm diameter) were produced by removing all above and below ground plant material to a depth of 10 cm. The soil was sieved using a 1 cm mesh screen to remove all perennial organs, then replaced. Eight plots were produced for each site, date and size. A randomized block design was used where plots were located within eight $16 \times 20 \text{ m}^2$ blocks of homogeneous soil and vegetation separated by 10 m borders of undisturbed vegetation within a 0.75 ha area at each site. For each recolonization date, one plot of each of the three sizes was randomly assigned to one of the $20 \times 16 \text{ m}^2$ cells within each block. The result was that the blocks and plots were separated by undisturbed vegetation to allow each plot to be near a source of propagules from the undisturbed plant community.

Data collection and analysis

The number of plants were counted and the percentage canopy cover was estimated by species in early June and late July (1985, 1986) on each of the ant mounds, animal burrows and artificial plots. The sampling dates were chosen to correspond to the maximum development of cool and warm season species. Density and cover values were obtained within concentric circles of 25, 50 and 100 cm in diameter to determine the relative location of each plant within each of the disturbed areas. Total density on each disturbance was found by summing the densities of each circle. The short term effects of the disturbance characteristics on plant recovery were analyzed using data collected one year after plant recovery began on the disturbed areas. Therefore, the data collected for the two sampling dates in 1985 were used for the September (1984) disturbances, while the data collected in 1986 were used for the disturbances of the three dates in 1985.

Because plant recovery on western harvester ant mounds and animal burrows was only monitored on coarse textured soils and the average surface area of ant mounds (0.92 m^2) and burrows from small animals (0.98 m^2) were most similar in size to the 100 cm diameter artificial plots (0.78 m^2), the density and canopy cover of plants on ant mounds and animal burrows were compared with the 100 cm diameter artificial plots on the site with coarse textured soil. The effects of the location of the disturbance by soil type, recolonization date and size were evaluated using the data from the artificial plots.

Analysis of variance was used to evaluate the effects of disturbance type, location by soil texture, date and size on the density and cover of four groups: (1) all plants, (2) perennial grasses and sedges, (3) perennial forbs, shrubs and succulents, and (4) annual grasses and forbs. Tukey's *Q* values were used to compute least significant ranges (LSR) and to evaluate the significantly different means at the $P < 0.05$ level (Sokal & Rohlf 1981).

The composition of the undisturbed plant communities (controls) was determined using fifty 0.25 m^2 quadrats randomly positioned on transects in the vicinity of the disturbances at each of the three sites (artificial plots: coarse and fine textured soils [Coffin & Lauenroth 1989]; ant mound site [Coffin & Lauenroth unpublished]). The density and cover values for the plant communities on the site with coarse textured soil and the ant mound site were used as the control for the effects of disturbance type and seasonality. Because the animal burrows were located in an area that included the ant mound site, the control for ant mounds also represented the control for animal burrows. The number of individuals were counted and canopy cover by species was estimated for each quadrat. The data were collected at the same time as for the disturbances (early June and late July, 1985 and 1986). The values for the four sampling dates were used in an analysis of variance to evaluate the effect of soil type on the density and cover of the four groups of species for the

undisturbed plant communities.

RESULTS

The undisturbed plant communities of the ant mound site and the sites with coarse and fine textured soils for the artificial plots were typical of short-grass communities (Sims *et al.* 1978) by having greater than 60% of their total density and 80% of their total cover attributed to perennial grasses and sedges (Table 1). The plant communities were dominated by the perennial grass, *Bouteloua gracilis* which contributed greater than 70% to the total cover. Other important perennial grasses and sedges were *Carex heliophila* Mack. (sunsedge) and *Buchloe dactyloides* (Nutt.) Engelm. (buffalograss). [Nomenclature follows McGregor (1986)].

The plant communities at the site with coarse textured soil and the ant mound site were similar and significantly different from the plant community at the site with fine textured soil for all groups except perennial grasses and sedges. Density and cover of annuals [primarily *Vulpia octoflora* = *Festuca octoflora* (Walt.) Rydb. (sixweekgrass)] were significantly higher on the site with fine textured soil, while the density and cover of perennial forbs, shrubs and succulents were significantly higher on the other two sites. The succulent, *Opuntia polyacantha* Haw. (plains pricklypear) and the perennial forb, *Sphaeralcea coccinea* (Pursh) Rydb. (scarlet globemallow) were important contributors to density and cover on all three sites, while the shrubs *Chrysothamnus nauseosus* (Pall.) Britt. (rabbitbrush), *Gutierrezia sarothrae* (Pursh) Britt & Rusby (broom snakeweed) and *Atriplex canescens* (Pursh) Nutt. (four wing saltbush) occurred primarily on the site with coarse textured soil and the ant mound site.

Species composition and disturbance type

The density and cover of the four groups of species were different for the three disturbance types, although the species found on the disturbances were similar. The first year after western harvester ant mounds were vacated, most of the density (>70%) and canopy cover (>80%) of plants on the mounds were perennials (Figures 1;2), including forbs (*Sphaeralcea coccinea*, *Oenothera caespitosa* Nutt. (evening primrose) and *Picrodeniopsis oppositifolia* (Nutt.) Rydb. (plains bahia), the succulent (*Opuntia polyacantha*), the subshrub [*Artemisia frigida* Willd. (fringed sagewort)], the grasses [*Sporobolus cryptandrus* (Torr.) A. Gray (sand dropseed) and *Sitanion hystrix* Nutt. (squirreltail)] and the sedge *Carex heliophila*. Important annual species were *Vulpia octoflora*, *Plantago patagonica* Jacq. (Patagonian plantain) and *Lepidium densiflorum* Schrad. (prairie pepperweed). For most dates, the density and cover of perennial forbs, shrubs and succulents on ant mounds were greater than

Table 1. Average density and canopy cover of four groupings of species for three undisturbed plant communities.

	Fine Textured Soil ¹	Coarse Textured Soil ¹	Ant Mound Site ²
Density (no./m ²)			
Perennial grasses and sedges	86	81	72
Perennial forbs, shrubs and succulents	8*	16	19
Annual grasses and forbs	41*	14	10
Total	134*	112	101
Canopy Cover (%)			
Perennial grasses and sedges	38	38	41
Perennial forbs, shrubs and succulents	4*	7	8
Annual grasses and forbs	2*	1	1
Total	44*	46	49

* indicates significance at $P < 0.05$ among sites for each species group

¹ from Coffin & Lauenroth (1989)

² from Coffin & Lauenroth (unpublished)

perennial grasses and sedges while the reverse was true for the surrounding undisturbed vegetation.

Most density (71%) and cover (53%) of plants on the mound of soil from small animal burrows were from perennial grasses and sedges (Figures 1;2). Large contributions to density (23%) and cover (44%) were also made by perennial forbs, shrubs and succulents. The same species of perennial plants were found on animal burrows as for ant mounds with the addition of a large contribution to cover by *Bouteloua gracilis* (20%). Relatively few annuals were found on the burrows and were primarily the forb species, *Chenopodium album* L. (lamb's quarters). Although the density of perennial grasses was significantly higher on the burrows than in the surrounding vegetation, the cover of perennial grasses was significantly lower (Figures 1;2).

In contrast to ant mounds and animal burrows, the densities of annuals, perennial grasses and perennial forbs, shrubs and succulents were comparable within and among dates on the 100 cm diameter artificial disturbances on the site with coarse textured soil, while the total densities of plants were comparable among dates (Figure 1). Greater than 43% of the total cover on the plots was due to annuals and more than 33% was due to perennial forbs, shrubs and succulents (Figure 2). Important species on artificial plots were the perennials: *Sphaeralcea coccinea*, *Oenothera caespitosa*, *Picrodeniopsis oppositifolia*, *Carex heliophila*, *Sporobolus cryptandrus*, *Sitanion hystrix* and *Buchloe dactyloides*, and the annuals: *Vulpia octoflora*, *Lepidium densiflorum*, *Plantago patagonica* and *Chenopodium album*. Significantly lower density and cover of perennial grasses occurred on the artificial plots than for the surrounding undisturbed vegetation and for most dates, the cover of annuals was significantly higher on the plots than for the controls.

Disturbance type and recolonization date

The highest total density (228 plants/m²) and canopy cover (30%) of the three disturbance types were found on animal burrows (Figure 3). For most dates, ant mounds had intermediate density (66-227 plants/m²) and cover values (14-25%) while artificial plots had the lowest density (29-70 plants/m²) and cover (8-20%). Significant effects of recolonization date were the result of low cover values on artificial plots produced in September.

The density (162 plants/m²) and cover (16%) of perennial grasses and sedges on animal burrows were significantly higher than on ant mounds or artificial plots (Figure 4). Most of the perennial grasses and sedges on the three disturbance types were from individuals of the rhizomatous species, *Carex heliophila*. For most dates, the lowest density and cover values were found on the artificial plots. The low cover values for the September artificial plots (0.2%) were the significant date effects for perennial grasses and sedges.

Ant mounds and animal burrows had higher density (30-116 plants/m²) and cover (9-17%) of perennial forbs, shrubs and succulents for all recoloniza-

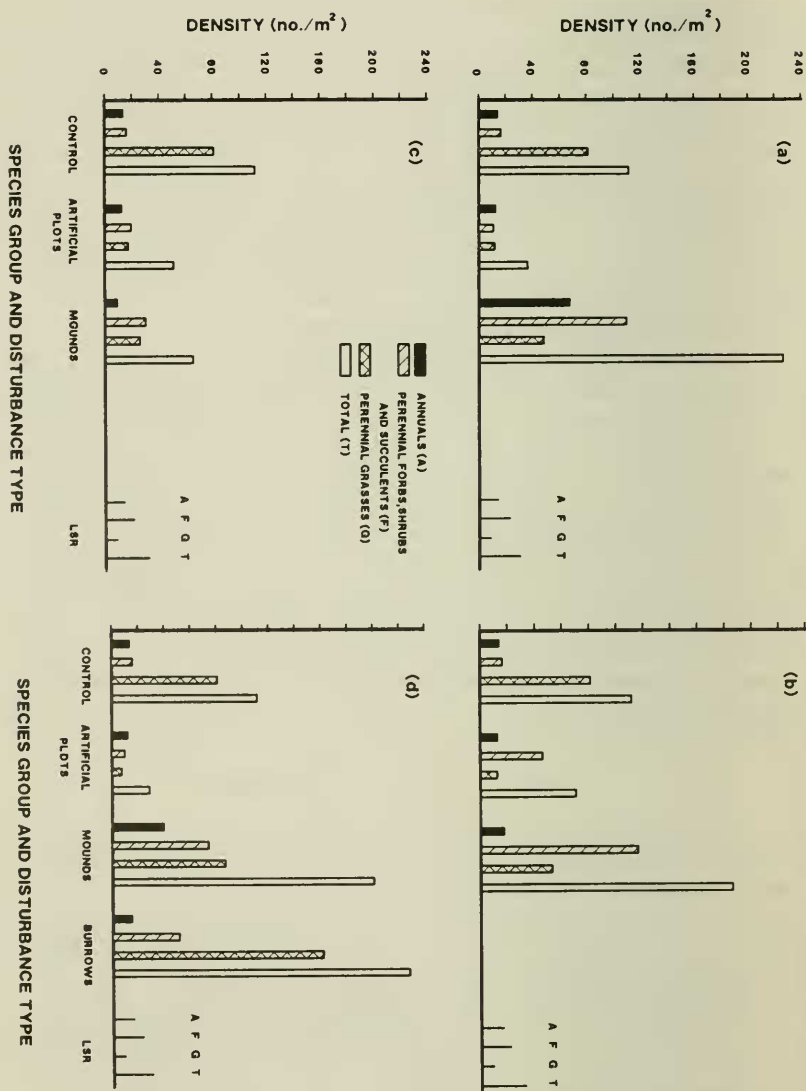


Figure 1. Density of plants of four groups of species for three disturbance types and the control for four recolonization dates (a) September, 1984 (b) March, 1985 (c) May, 1985 (d) July, 1985. Use LSR_A for significance of annuals between disturbance types and the control and within dates, LSR_F for perennial forbs, shrubs and succulents, LSR_G for perennial grasses and sedges, and LSR_T for total density.

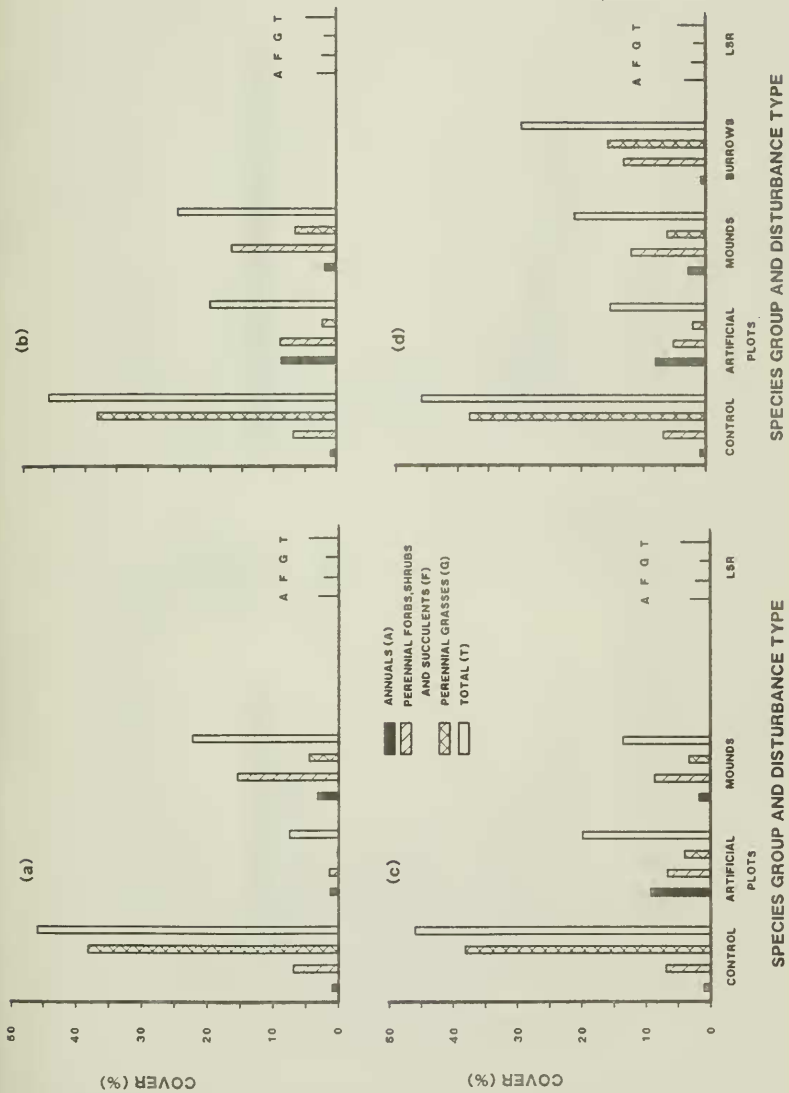


Figure 2. Cover of plants for four groups of species for three disturbance types and the control for four recolonization dates (a) September, 1984 (b) March, 1985 (c) May, 1985 (d) July, 1985. For explanation on use of significance ranges (LSR) see Figure 1.

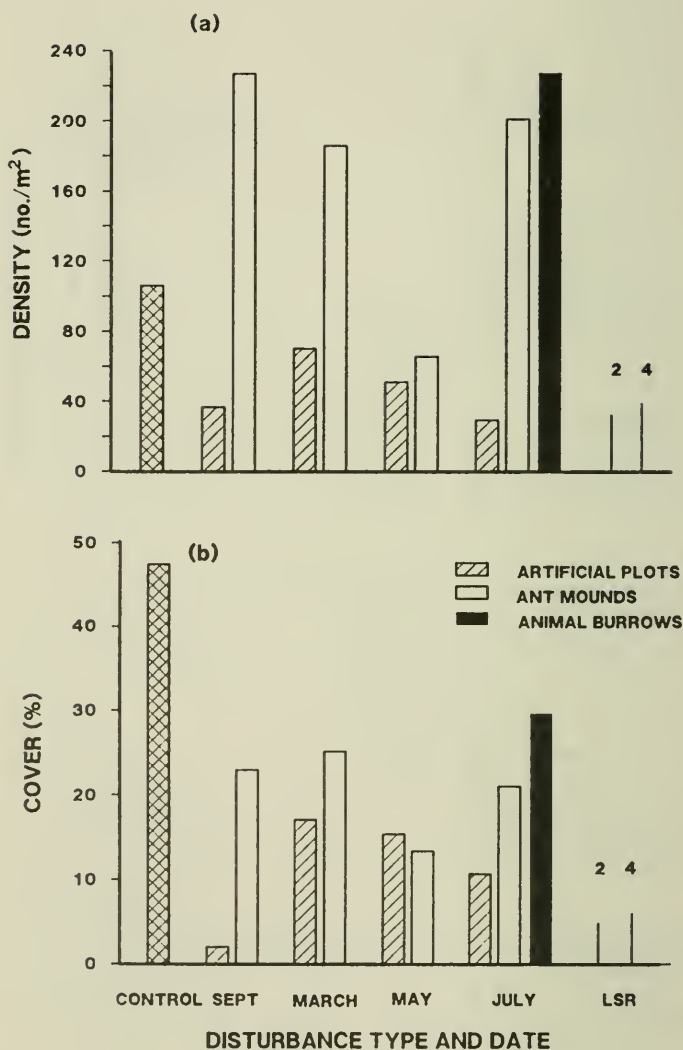


Figure 3. Density and cover of plants for three disturbance types and the control for four recolonization dates. Use LSR_2 for significance of type within dates and LSR_1 for significance of date within types.

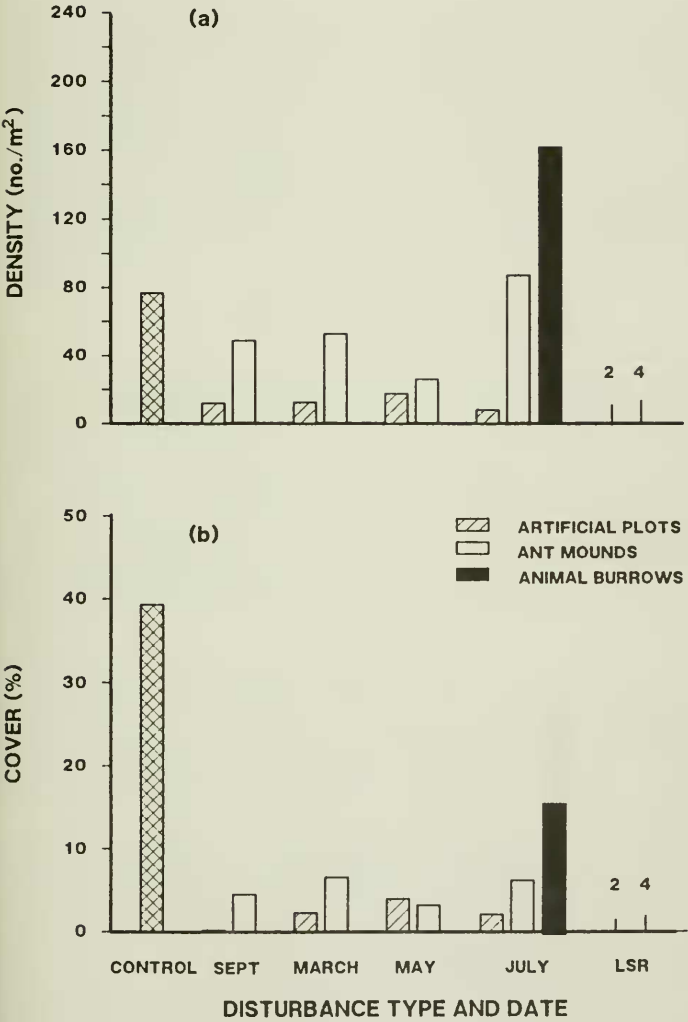


Figure 4. Density and cover of perennial grasses and sedges for three disturbance types and the control for four recolonization dates. For explanation on use of significance ranges (LSR) see Figure 3.

tion dates than the artificial plots (Figure 5). *Sphaeralcea coccinea* was the most important species in this group for the three disturbance types. Significant date effects were the result of high densities on the March plots and low cover values on the September plots. The density of annual plants was comparable on the three disturbance types, except for the high densities of annuals found on ant mounds vacated in September (Figure 6a). The percentage cover of annuals was significantly higher on artificial plots than on mounds or burrows for all dates except September (Figure 6b). Most of the cover on the artificial plots was attributed to two species, *Lepidium densiflorum* and *Vulpia octoflora*.

Disturbance location, date and size

Similar species were found on the artificial plots at the sites with fine and coarse textured soils, although the density and cover values of the four groups of species were significantly different. The total density of plants on artificial plots at the site with fine textured soil (33-211 plants/m²) was higher for all sizes and all dates than the density of plants on plots at the site with coarse textured soil (34-81/m²) (Figure 7). Densities on the disturbed plots were comparable for most dates and sizes within each site. The percentage canopy cover on artificial plots at the site with fine textured soil was significantly greater than plots at the site with coarse textured soil for all dates except September (Figure 7c).

Similar density and cover values of perennial grasses were found for both sites, although the values on the plots were less than on the controls (Figure 8). The 50 cm diameter plots had significantly higher density values, due to *Carex heliophila* on the site with fine textured soil and *Buchloe dactyloides* on the site with coarse textured soil, than the 100 cm or 150 cm diameter plots for both sites and most dates.

The density of perennial forbs, shrubs and succulents on the artificial plots for both sites were comparable to or significantly greater than the controls (Figure 9a,b). The March plots on the site with fine textured soil had significantly greater density values for all three plot sizes than the plots for the other dates primarily because of differences in the densities of *Sphaeralcea coccinea* (Figure 9b). In most cases, the 50 cm diameter plots had the smallest density values of the three sizes within a date and site. Although the percentage cover of perennial forbs, shrubs and succulents was significantly different for the two controls, significant site differences were not found for the cover of plants on the plots (Figure 9c). The plots produced in September had significantly smaller cover values for all three sizes than plots for the other three dates.

The density and cover of annuals was higher for the three plot sizes on the site with fine textured soil and the control vegetation than for plots on the site with coarse textured soil (Figure 10a,b). Significantly greater density and

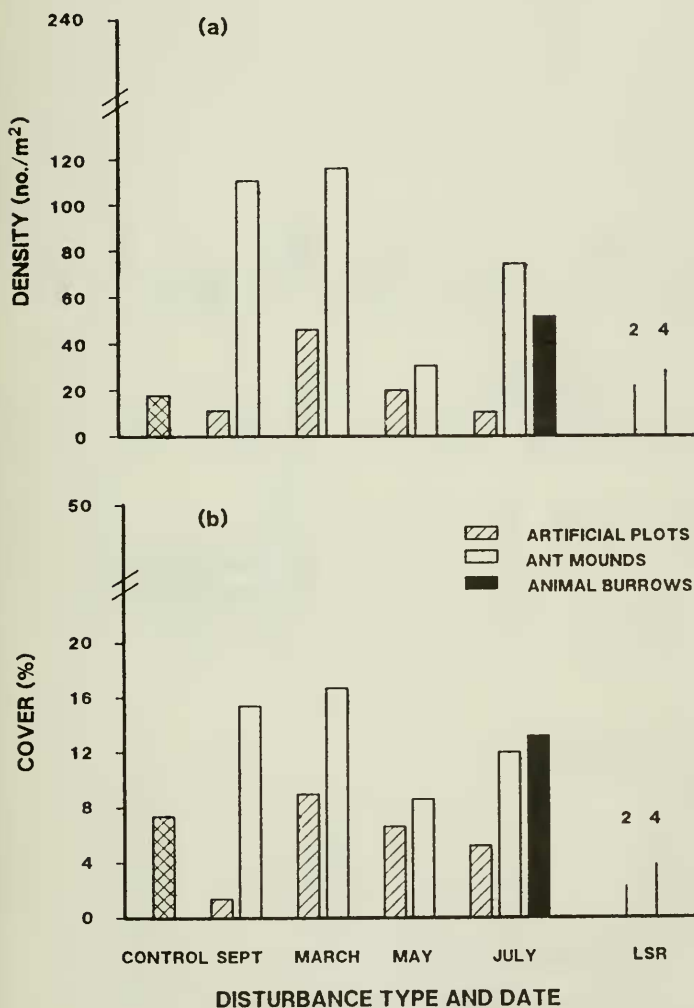


Figure 5. Density and cover of perennial forbs, shrubs and succulents for three disturbance types and the control for four recolonization dates. For explanation on use of significance ranges (LSR) see Figure 3.

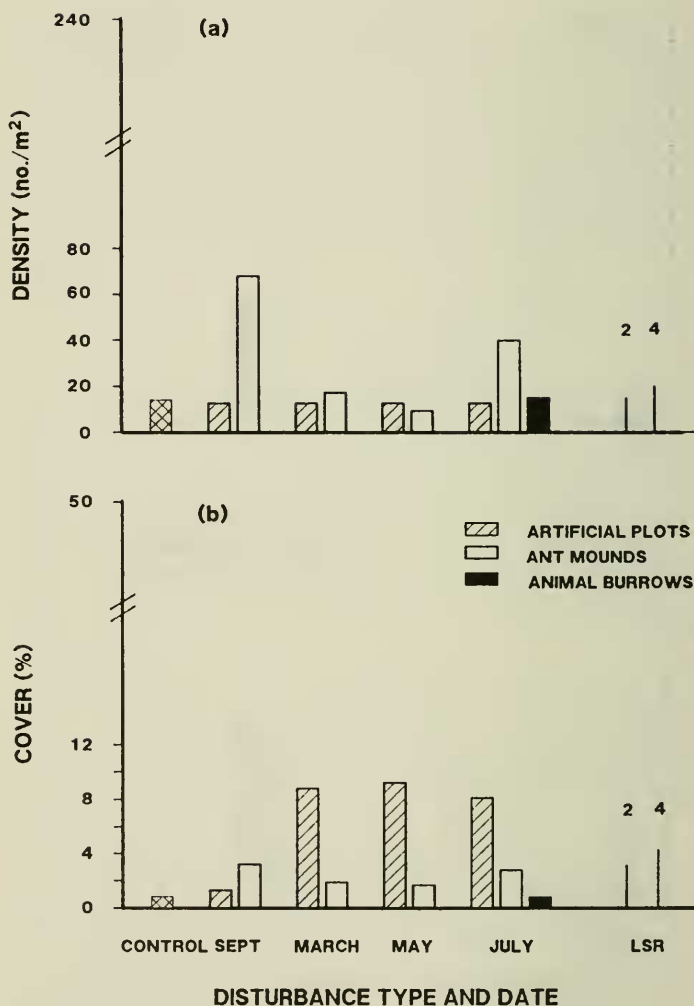


Figure 6. Density and cover of annuals for three disturbance types and the control for four recolonization dates. For explanation on use of significance ranges (LSR) see Figure 3.

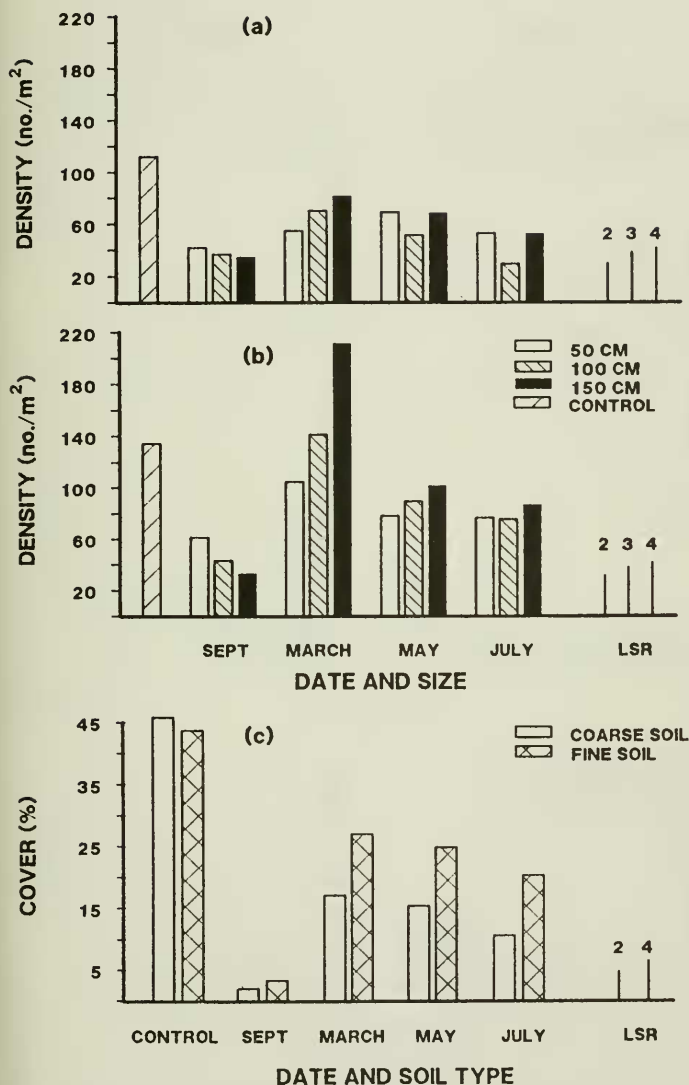


Figure 7. Density of plants on artificial plots of three sizes for four dates, and the control for two sites (a) coarse textured soil (b) fine textured soil. (c) Cover of plants on artificial plots of three sizes for four dates. Use LSR₂ for significance of site within size and date, LSR₃ for size within site and date, and LSR₁ for date within site and size.

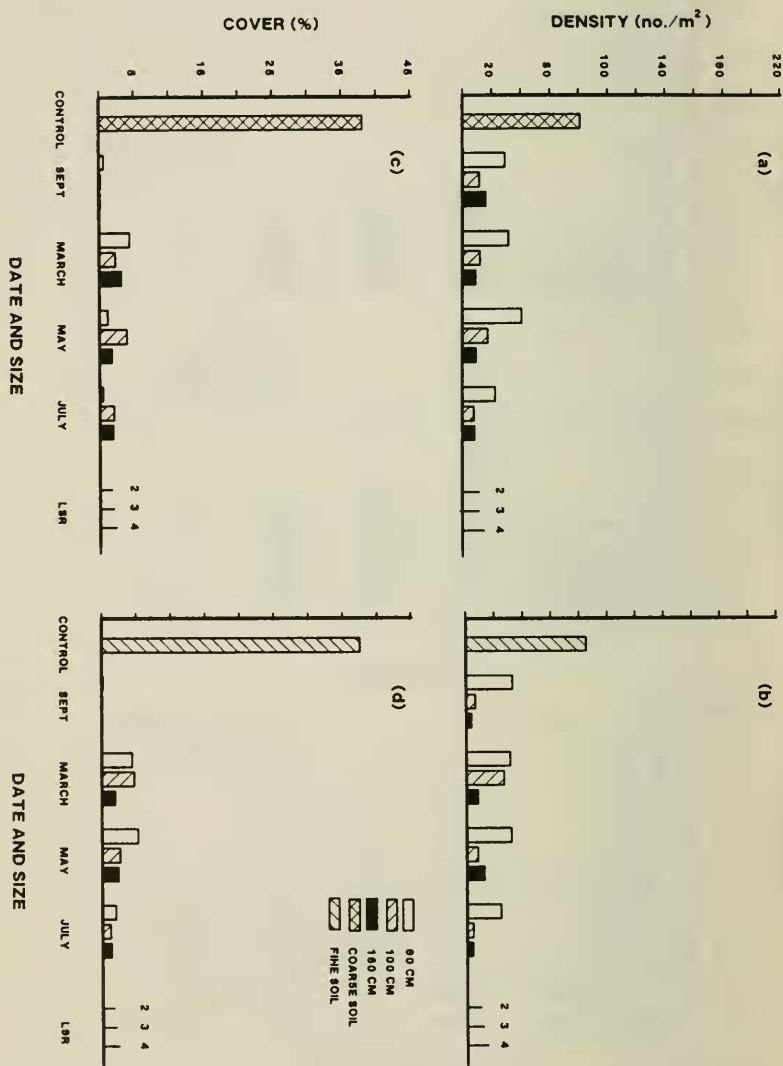


Figure 8. Density of perennial grasses and sedges on artificial plots of three sizes for four dates, and the control for two sites (a) coarse textured soil (b) fine textured soil. Cover of perennial grasses on artificial plots of three sizes for four dates, and the control for two sites (c) coarse textured soil (d) fine textured soil. For explanation on use of significance ranges (LSR) see Figure 7.

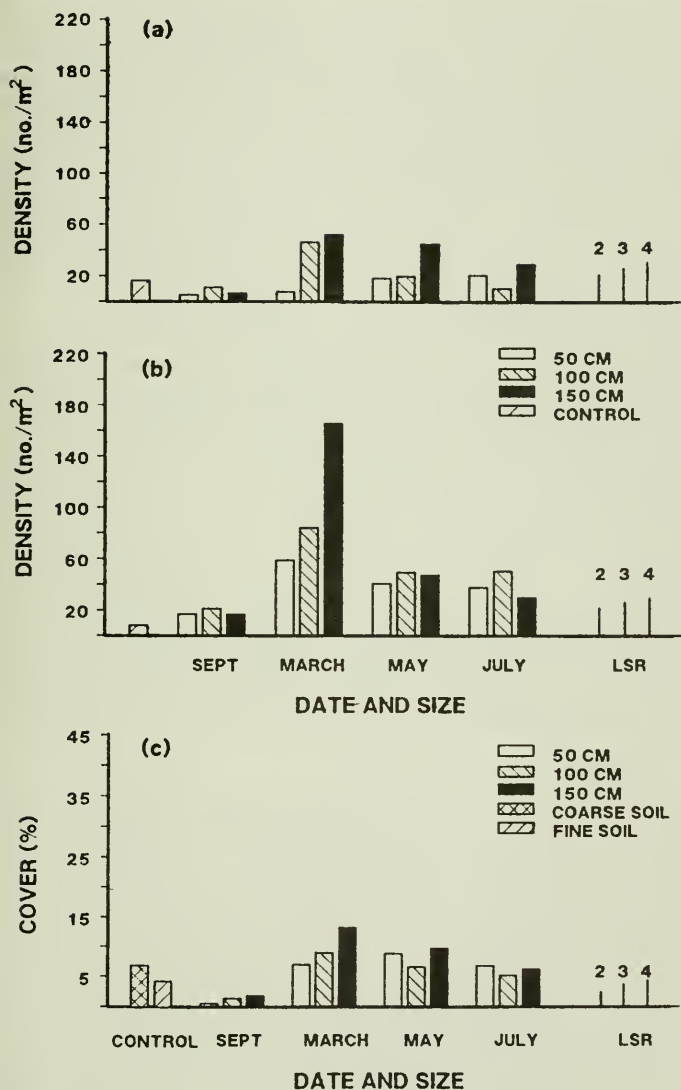


Figure 9. Density of perennial forbs, shrubs and succulents on artificial plots of three sizes for four dates, and the control for two sites (a) coarse textured soil (b) fine textured soil. (c) Cover of perennial forbs, shrubs and succulents on artificial plots of three sizes for four dates, and the control for two sites by soil texture. For explanation on use of significance ranges (LSR) see Figure 7.

cover values of annuals (primarily *Lepidium densiflorum* and *Chenopodium album*) were found on the 150 cm diameter plots than on the 50 cm diameter plots for the site with fine textured soil. The September plots had significantly lower cover values of annuals than plots for the other three dates (Figure 10c).

An analysis based on the density and cover of plants located in the 50 cm diameter center circle of each artificial plot was conducted to further evaluate the effects of disturbance size on plant recovery. Other factors besides perimeter and surface area, such as microenvironmental gradients and the ability of plants to disperse over the entire plot, may change as plot size changes, and would be indicated by a difference in the density and cover of plants in the center of the different sizes of plots.

The total density of plants located in the center circle of each plot was higher on the 50 cm diameter plots than the 100 cm or 150 cm diameter plots for both sites and most dates (Figure 11a,b). Although total density was higher on the 50 cm diameter plots, percentage canopy cover was significantly higher on the 100 cm (18%) and 150 cm (19%) than on the 50 cm diameter plots (11%). Significantly higher density and cover values were found for perennial grasses and sedges (primarily *Carex heliophila* and *Buchloe dactyloides*) for the 50 cm diameter plots than for the 100 cm or 150 cm diameter plots on both sites (Figure 12). Size was not a significant factor for the density or cover of perennial forbs, shrubs and succulents except for the high density and cover values on the March 150 cm diameter plots, due to *Sphaeralcea coccinea* (Figure 13). Although the densities of annuals were not affected by disturbance size, the cover values were significantly higher on the 100 cm (10%) and 150 cm diameter plots (11%) than on the 50 cm diameter plots for all dates (3%).

DISCUSSION

The species composition on the two naturally occurring disturbances (western harvester ant mounds and small animal burrows) were similar one year after plant recovery began, and were different from the composition on the artificially produced disturbances. This distinction between natural and human caused disturbances was also found for grasslands and savannas of the Serengeti National Park (Belsky 1987). The high density and cover of perennials on ant mounds and animal burrows indicate that perennial organs, such as rhizomes of *Carex heliophila* and tap roots of *Sphaeralcea coccinea*, were not killed by the clipping activity of harvester ants or the pile of soil from burrowing animals. Similar growth of perennial grasses and forbs on badger mounds was observed in the first growing season in a tallgrass prairie (Platt 1975).

The recolonization of western harvester ant mounds was primarily by perennials, and the density of annuals on the mounds was significantly greater than on animal burrows and most artificial plots. The activities of western harvester ants may affect the recovery of plants on abandoned mounds in several

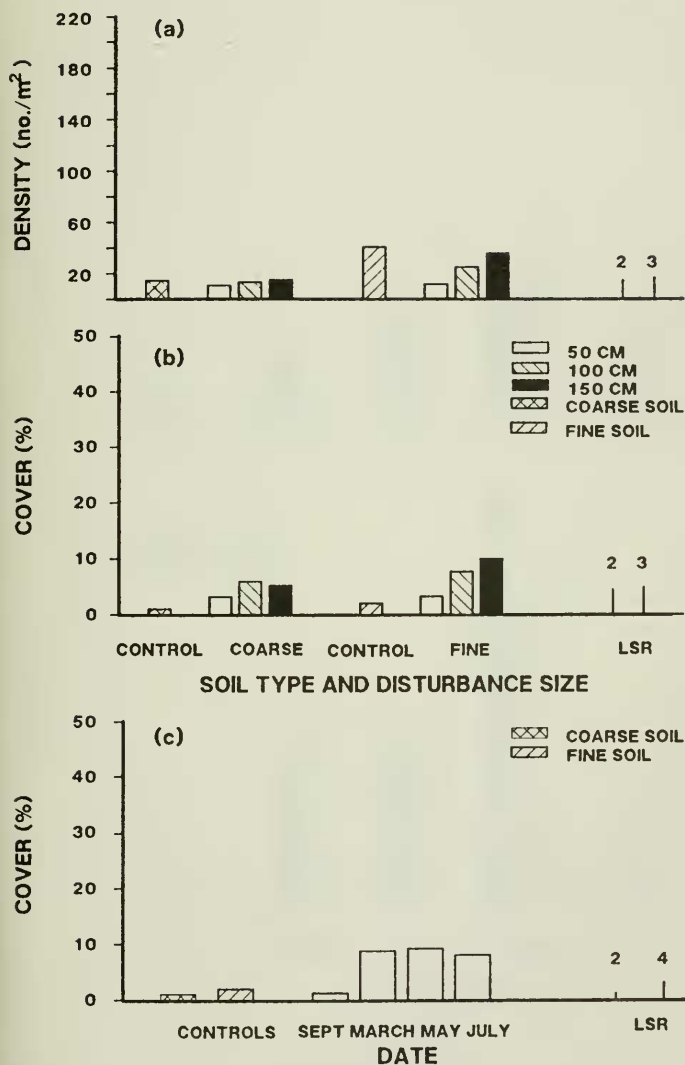


Figure 10. (a) Density of annuals on artificial plots of three sizes for four dates, and the control for two sites by soil texture. (b) and (c) Cover of annuals on artificial plots of three sizes for four dates, and the control for two sites by soil texture. For explanation on use of significance ranges (LSR) see Figure 7.

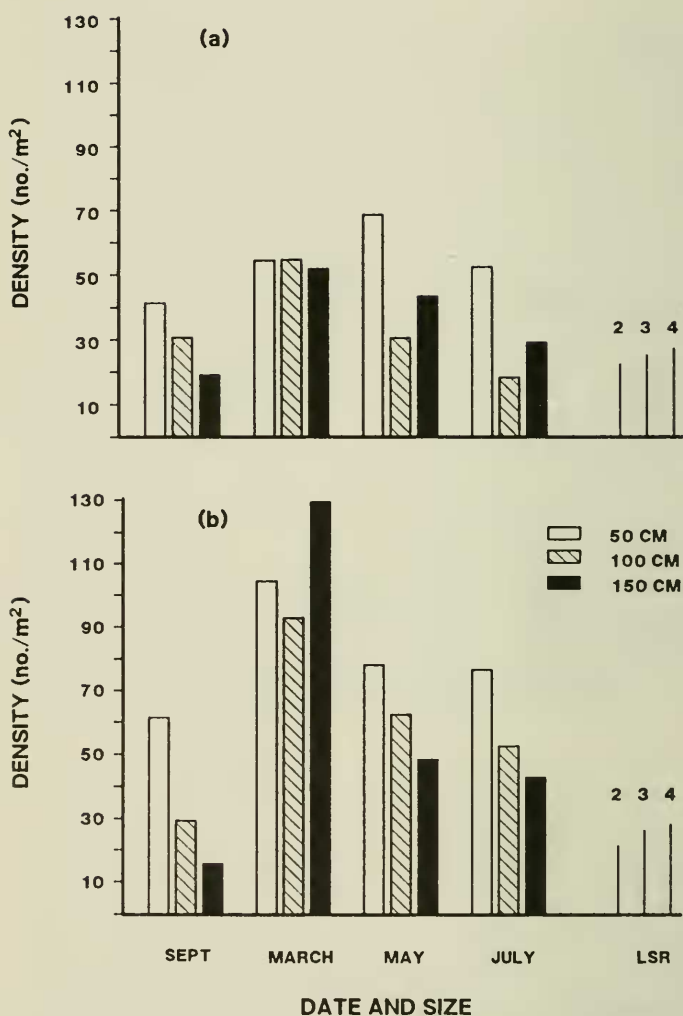


Figure 11. Density of plants in the center 50 cm diameter circle of artificial plots of three sizes for four dates and two sites (a) coarse textured soil (b) fine textured soil. For explanation on use of significance ranges (LSR) see Figure 7.

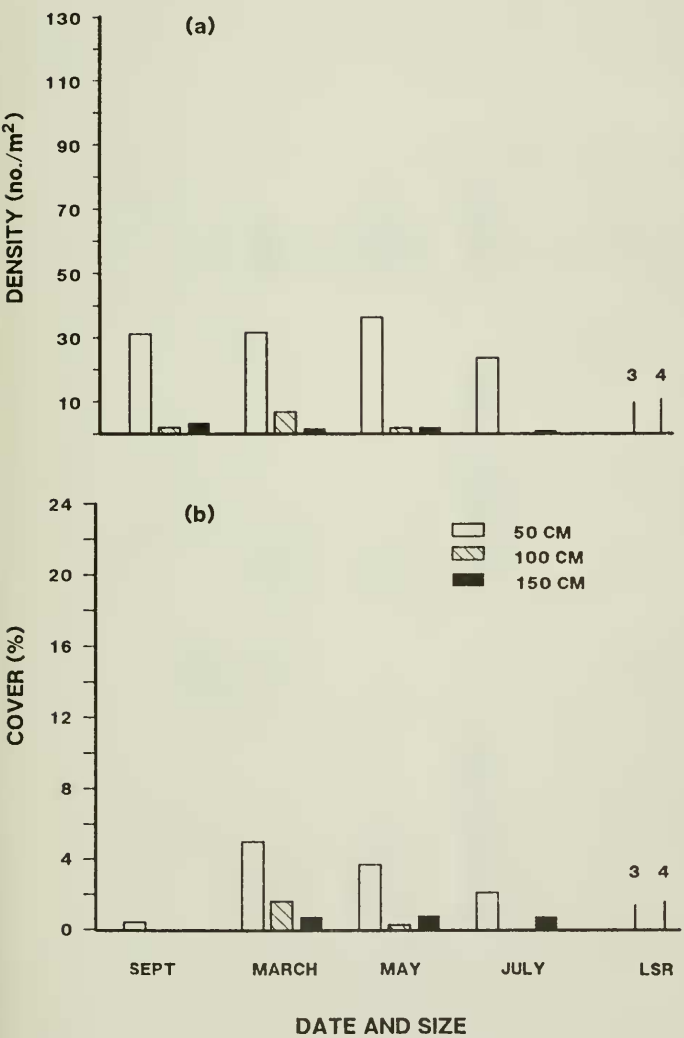


Figure 12. Density and cover of perennial grasses and sedges in the center 50 cm diameter circle of artificial plots of three sizes for four dates. Use LSR_3 for significance of size within date and LSR_4 for date within size.

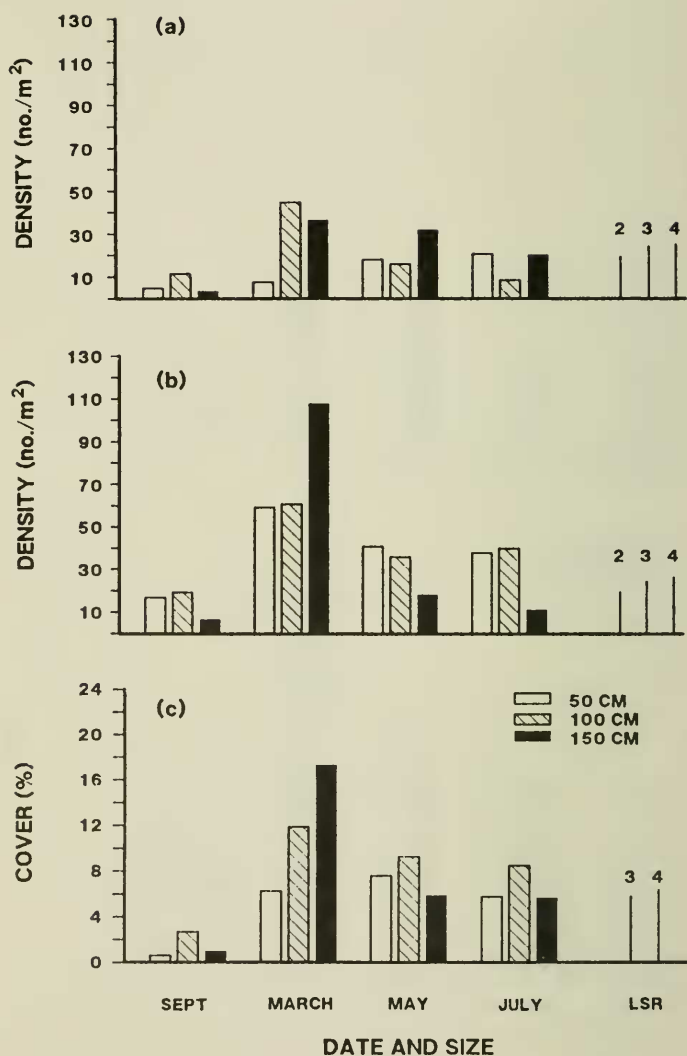


Figure 13. Density of perennial forbs, shrubs and succulents in the center 50 cm diameter circle of artificial plots of three sizes for four dates and two sites (a) coarse textured soil (b) fine textured soil. For explanation on use of significance ranges (LSR) see Figure 7. (c) Cover of perennial forbs, shrubs and succulents in the center 50 cm diameter circle of artificial plots of three sizes for four dates. For explanation on use of significance ranges (LSR) see Figure 12.

ways due to the interactions of ants with their environment during the 30-60 years that a colony may inhabit a nest site (Wiens 1976; Coffin & Lauenroth unpublished). The foraging and clipping activities of the ants affect the microenvironmental conditions on the nest as well as the availability of reproductive and vegetative propagules.

Nutrients and seeds are concentrated in a nest as a result of the foraging and storage of seeds and other organic materials in underground chambers by harvester ants, and soil water is significantly higher ($P < 0.05$) in a nest than at points away from the nest due to the clipping of all plants from the mound (Rogers 1974; Rogers & Lavigne 1974). The significantly greater ($P < 0.05$) standing crop of plants surrounding a mound compared to points located away from the mound (Rogers & Lavigne 1974) may also result in an increased availability of seeds and vegetative propagules to an abandoned mound compared to disturbances that are recolonized immediately after being produced (artificial plots and animal burrows). The number of germinable seeds found near the soil surface of mounds in September, 1984 (6756 seeds/m² from Coffin & Lauenroth unpublished) was significantly greater ($P < 0.05$) than the number of seeds in the soil at the site with coarse textured soil for the same date (2748 seeds/m² from Coffin & Lauenroth 1989). The length of time these conditions persist on an abandoned mound is unknown. However, the largest effects on plant recovery most likely occur in the short term.

The 6% cover by the dominant plant species, *Bouteloua gracilis*, on animal burrows was primarily due to the vegetative growth of *B. gracilis* plants partially covered by soil. *Bouteloua gracilis* was not found in significant amounts on ant mounds or artificial plots. These results suggest that the time required for *B. gracilis* to dominate the plant community on animal burrows will be less than for ant mounds or artificial plots, and less than the estimated recovery time of greater than 50 years for *B. gracilis* to dominate abandoned agricultural fields (Reichhardt 1982). The recovery time for abandoned fields was based on the observation that it took 33 years for *B. gracilis* to occur on the fields and another decade to reach 2% in frequency of occurrence (Reichhardt 1982).

In contrast to ant mounds and animal burrows, the majority of the cover on the artificially produced disturbances for the sites with coarse and fine textured soils, and most dates and sizes, was attributed to annuals. This is similar to plant communities found on old roads and abandoned agricultural fields in the shortgrass steppe region within five years after the beginning of plant recovery (Shantz 1917; Costello 1944; Judd 1974; Reichhardt 1982). Perennials colonized the artificial plots in the first year as indicated by the comparable densities of annuals, perennial grasses and sedges, and perennial forbs, shrubs and succulents.

The recolonization date and size of the disturbance had important effects on the density and cover of plants on artificial plots. The effects of recoloniza-

tion date on short term successional dynamics are due to interactions between the availability of propagules to the site and the microenvironmental conditions on the site relative to the requirements for germination, establishment and growth of the propagules (Sousa 1984). The low cover of annuals and perennials on artificial plots produced in September may be a combination of: (1) the seasonal dynamics in the relatively few germinable seeds stored in the soil at the two sites (964 seeds/m² averaged over two years from Coffin & Lauenroth 1989), (2) the low and variable patterns of precipitation found in the shortgrass region (Sala & Lauenroth 1982), and (3) the timing of the precipitation events relative to factors such as temperature. Because of the variability in precipitation within and among years, conducting the study in another year would most likely indicate the timing of the disturbance to have important effects on plant recovery, however, the specific effects observed in this study may not occur.

Although annuals and perennials responded similarly to the effects of recolonization date, they responded differently to disturbance size. The size of the disturbance may be important to the availability of propagules to the disturbed site and the resources available to the propagules. As disturbance size increases, propagules must disperse over larger distances to colonize the entire disturbed area, while competition from plants around the edge increases as the size of the disturbance decreases (Sousa 1984).

The source of propagules for annuals included seeds stored in the soil and the dispersal of seeds onto the plot. The density of annuals was not affected by disturbance size while the effects of competition by plants surrounding the plots on the growth of annuals was indicated by the significantly smaller cover values on the smallest compared to the largest plots.

Perennials may recover either from seedling establishment or vegetative growth. Relatively few perennial grass or perennial forb, shrub and succulent seeds were found stored in the soil compared to annual seeds (Coffin & Lauenroth 1989). Most of the perennials on the plots were the result of vegetative growth by *Carex heliophila*, *Buchloe dactyloides* and *Sphaeralcea coccinea*. The recovery of *C. heliophila* by rhizomes and *B. dactyloides* by stolons occurred as ingrowth from the edge of the plots. The greater perimeter to area ratio of small compared to large plots (Miller 1982; Sousa 1984) resulted in significantly greater cover and density values of perennial grasses and sedges on the smallest plots for most dates and both sites.

The cover of the perennial forb, *Sphaeralcea coccinea*, responded similarly to disturbance size as annuals by having the highest values in the center circle of the largest plots, or the farthest distance from potential competitive interactions with plants in the surrounding undisturbed community. Although the density of annuals was not affected by disturbance size, the density of *S. coccinea* responded similarly to the cover values. The recovery of this important forage species (Hyder *et al.* 1975) was primarily from deep tap roots either

from plants at the edge of the plot or by regrowth of plants on the plot.

The interaction between disturbance size, recolonization date and location by soil texture was also important to the cover and density of *Sphaeralcea coccinea*. The period of growth of this species (April and early May from Dickinson & Dodd 1976) corresponds to the significantly greater density and cover values on the largest plots cleared in March on the site with fine textured soil for perennial forbs, shrubs and succulents than for plots of the other dates. Similar results on the importance of the timing of the availability and growth of propagules relative to the seasonality of the disturbance were found for the recovery of an annual grassland following small disturbances (Hobbs & Mooney 1985).

Although the long term monitoring of the disturbed sites for the three disturbance types and their associated characteristics is necessary to evaluate the time required for each disturbed area to be dominated by a shortgrass plant community, the results after one year of recovery suggest that animal burrows will have the most rapid recovery time of the disturbance types studied because of the presence of *Bouteloua gracilis* and other perennials on the burrows. Artificial plots, and in particular the largest plots, will have the slowest recovery time since relatively few perennials were found on the plots compared to ant mounds or animal burrows.

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